Summary of

Tree-Breeding Experiments

By The Northeastern Forest Experiment Station
1947-1950

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INTRODUCTION

THE TREE-BREEDING WORK of the Northeastern Forest Experiment Station has its roots in a project started in 1924 by the Oxford Paper Company of Rumford, Maine, to develop fast-growing poplars that would be suitable for pulpwood. The initial tree-breeding work in this project was done by A. B. Stout and Ernst J. Schreiner, most of it at the New York Botanical Garden and in the city parks of Rochester, N. Y. The hybrids developed were placed in test plantations near Rumford, Maine.

In 1936 the work was taken over by the Northeastern Forest Experiment Station at New Haven, Conn. The poplar-breeding and testing work was continued under the direction of E. J. Schreiner. The scope of the project was enlarged to include the major northeastern tree genera, and exploratory work was started. Techniques were worked out, potentially valuable hybrids were produced, and the groundwork was laid down for future breeding work in these genera.

Early in World War II the Northeastern Station at New Haven was deactivated, and its personnel were transferred to

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[1] STATIONED AT THE MORRIS ARBORETUM, PHILADELPHIA, IN COOPERATION WITH THE UNIVERSITY OF PENNSYLVANIA.

the Allegheny Forest Experiment Station at Philadelphia. The tree-breeding project was suspended (except for bare maintenance work) for the duration of the war.

At the end of the war, the Allegheny Station and its research territory were reorganized and expanded, and the new organization was renamed the Northeastern Forest Experiment Station, with headquarters in Philadelphia (later moved to Upper Darby, a Philadelphia suburb). At this time the tree-breeding research was resumed and expanded.

The earliest poplar hybrids and the newer maple, pine, and other hybrids from the 1936-41 experiments were outplanted at various locations throughout the Northeast, where they remain under observation. Results of the poplar studies and the other early experiments have been reported by Schreiner (34)[2] and others.

Meanwhile, studies of other species were resumed along the lines of the 1936-41 studies. Most of these studies were made by the author, in the vicinity of Philadelphia. This report outlines the progress that has been made in the period 1947-50.

OBJECTIVES

The objectives of the tree-breeding research project are (1) to produce superior types of trees for forest planting in the Northeast, and (2) to work out techniques for the genetic improvement of natural stands in the region. The improved types should be suitable for pulp or lumber production. Byproducts for erosion control, Christmas trees, wildlife plantings, and ornamentals are welcomed but are not sought after.

Plant breeding utilizes differences within or between species. Up to now we have had knowledge of few intraspecific differences to work with; so we have concentrated on crosses between species where the differences are apparent. As our knowledge of known differences within species becomes greater we shall increasingly utilize them in the breeding work.

A new variety for forest planting must be cheaply propagated. Except in the poplars and possibly a few other hardwoods such as birch and maple, we are interested mainly

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[2] UNDERLINED NUMBERS IN PARENTHESES REFER TO LITERATURE CITED, PAGE 43.

in seed propagation, for two reasons. First, the genera we are working with are moderately difficult to nearly impossible to root from cuttings; and grafting is expensive. Second, the uniformity resulting from clonal propagation often in itself results in serious disease and insect difficulties.

As yet there has been little opportunity for making selections within species. This means that even though a new hybrid individual may grow better than either of its parents it may still not represent the best hybrid obtainable from select parents of the species involved. In some instances the improvement achieved may be no greater than the improvement possible by selection within species. The initial hybrid, however, will point the way to the final product, which will entail selection previous to hybridization.

BREEDING MATERIAL

The breeding work has been done on trees in the Morris Arboretum of the University of Pennsylvania, Philadelphia; Andorra Nursery, Conshohocken, Pa.; Haverford College, Haverford, Pa.; Westtown School, Westtown, Pa.; Swarthmore College, Swarthmore, Pa.; and in various wild stands near Philadelphia.

Most of the pollens used have come from these same trees, but pollen was also obtained from trees in the Arnold Arboretum, Jamaica Plain, Mass., the arboretum of the Institute of Forest Genetics, Placerville, Calif., and from a few wild stands of certain species in the eastern United States.

Nomenclature of species studied follows Rehder (27), since many of the species are not listed in the U. S. Forest Service Check List of the Native and Naturalized Trees of the United States Including Canada (325 pp., Washington, D. C., 1944).

METHODS

Breeding techniques used in forest tree breeding have been described by Schreiner (32), Johnson and Bradley (18), and Cumming and Righter (6). In general the techniques described by these authors have been followed. However, a

number of refinements, such as washing catkins previous to pollen extraction, cutting of needles while applying bags, and use of double pollination bags, have been eliminated.

The techniques used for yellow-poplar differ in several respects from those described by Carpenter and Guard (5), as mentioned later in this report.

TYPES OF POLLINATIONS MADE

Three types of pollinations--self, intraspecific, and interspecific--were made on each female whenever possible. In addition, some bagged branches were left unpollinated and open-pollinated seed was collected from each female. Certain of these pollinations were dispensed with after the breeding behavior of an individual or of a species was well known.

The choice of species to be crossed was governed by (1) availability of flowering material, (2) closeness of taxonomic relationship, and (3) timber potentialities of the species for the Northeast. In the ashes, pines, and maples closeness of taxonomic relationship has proved a good indicator of species crossability; but in the spruces and oaks it has not.

Choice of parent within species was governed mostly by flowering and fruiting behavior of the individual trees, even though phenotypic and genotypic selection for growth performance and seed set is probably necessary in most cases.

BAGGING

Sausage-casing or vegetable-parchment bags were used to protect flowers from unwanted pollination. The bags were secured by putting a wad of cotton around the branch and tying the open end of the bag around this cotton.

Yellow-poplar flowers were emasculated (by removal of stamens and perianth), pollinated, and bagged in quick succession on the same day. In the maples (except boxelder) unopened flower buds were bagged several days before pollination. All other species were bagged when the flowers were slightly open (and probably receptive) but up to 10 days before any noticeable pollen shedding by nearby trees of the same species. Data from trees that were inadequately bagged have been omitted.

A few spruce and pine trees that set very little seed to open pollination have been worked without bagging. All trees so worked are indicated in the tables.

In recent years most bags used on pines have been applied on the current year's growth with no needle removal. The bags are relatively small (2 x 8 inches to 3 x 12 inches) and have caused little twig breakage.

Except where otherwise noted (sugar maple, European ash) emasculation was practiced where needed so that none of the control-pollinated branches was subject to accidental self-pollination.

Pollination bags were left on red and silver maples until seed maturity. With other species they were removed 1 to 3 weeks after pollination. There is evidence that the bags may be left on some species to advantage until seed maturity (42).

POLLEN COLLECTION, STORAGE, & TESTING

To collect pollen from conifers, male catkins were gathered from 1 to 3 days before normal anthesis; they were placed on paper indoors and allowed to dehisce. To collect pollen of oaks, ashes, and most maples, flowering branches about 1 foot long were brought inside, placed in water, and allowed to shed pollen onto paper. Pollen was not collected at all from Norway maple and related species of maple and yellow-poplar; freshly opened anthers were used as pollination brushes. Branches of late-flowering maple species were successfully forced in the greenhouse by as much as a month.

Pollen was stored at 25 or 50 percent relative humidity and 40° F. (10). The pollen was carried in the field without a desiccator. When fresh anthers were used as pollinating brushes, small flowering branches were kept in water in the refrigerator and removed as needed.

Pollen was stored for only a few days for most crosses, although for a few crosses storage up to 6 weeks was necessary. Pollen viability was tested in the laboratory (germination tests on 2 percent agar containing 10 percent sugar) for many of the conifer pollens, but in most cases viability was checked by making intraspecific crosses. These tests indicated that pollen of various species of maple, ash, pine, and spruce may be successfully stored for

at least 3 weeks under the proper conditions. Only with yellow-poplar and maple (when pollen of the early-flowering red maple was stored 6 weeks for use on late-flowering species) is it probable that low pollen viability was the principal cause of low seed set.

Pollen of many ash and maple species is often difficult to collect in large quantity. So attempts were made to extend these pollens by dilution with talc or lycopodium spores. Diluted and undiluted pollens gave similar seed sets.

POLLINATION

Pollinations were made during the following periods:

Maple, ash, oak.--From flower-bud opening and style exsertion until stigmatic withering, a period of 2 to 8 or more days per tree, depending on species.

Pine.--From complete visibility of the strobili until 1 or 2 days before complete scale closing, a period of 4 or 5 days per tree.

Fir, spruce.--From scale opening until the scales had nearly closed, a period of 2 to 5 or more days per tree, depending on species.

Yellow-poplar.--When the buds had dropped their bracts and were soft but not yet open at the tip, a period of ½ to 1 day per flower.

Except on yellow-poplar and Norway spruce, all the flowers on a tree (of the species herein reported) are at nearly the same stage at any one time.

Pollination of wind-pollinated species was effected by punching a small hole in the pollination bag, blowing pollen into the bag from a small medicine dropper, and sealing the hole with Scotch tape. With entomophilous species, pollination was effected by untying and removing the bag, brushing each stigma with a brush (most maples) or freshly opened anther (Norway and related maples, yellow-poplar), and replacing the bag. Each bagged branch was labelled with a copper-wired heavy paper label in which identifying holes were punched corresponding to a number recorded on a data sheet.

SEED COLLECTION & TREATMENT

In the first years all branches containing unripe fruit were cloth-bagged in mid-summer to prevent loss of seed. If done early in July, this bagging also prevented weeviling of oaks and ashes, but not of conifers. Conifer fruit is now collected without previous bagging.

The fruit was collected when the open-pollinated and filled seed on the same tree was clearly ripe as evidenced by shedding, cone opening, or condition of the embryo (solid, white in most species; solid, green in Norway and sugar maples.)

No simple way of separating filled yellow-poplar seed from empty seed was found without damaging the seed; so in this genus the amount of seed filling was judged entirely from germination behavior. For other species, seed filling was determined by pinch tests (ash, maple, fir), color (some hard pines), or by floating in 50 percent alcohol (spruce, pine). Short immersion in alcohol did not injure the seed.

Seeds of spring-fruiting maples were planted and seeds of oaks and fall-fruiting maples were stratified within 2 days of collection. Seeds of other genera were stratified as soon as convenient after extraction. Since 1949 the seeds have been treated with Semesan before stratification. Stratification was for 3 months in barely moist sphagnum in corked vials at 40° F. This was satisfactory for all species except white ash and European ash, for which warm-plus-cold stratification is needed (40), and fir, for which 120 days or more was needed.

After stratification, the seeds were sown in soil in the greenhouse. At 4 to 6 weeks the young seedlings were transferred to individual 2½-inch pots; 4 to 6 weeks later they were planted in the nursery. In some lots, especially from the 1947 pollinations, there was considerable loss from rot during storage, damping-off, or mice. Whenever numbers permitted, seedlings have been planted in randomized blocks in the nursery.

Hybridity of the seedlings has been judged from comparative seed sets and the characters of the progeny up to the age of 3 years (the oldest progeny). Usually an effort has been made to compare progenies from the same female parent, although this has not always been possible. Only combinations giving consistently high seed sets or progeny different from others from the same female parent are considered as hybrids.

RESULTS

ACER

In mid-March 1948, cut branches of several maple species were treated with 0.1 percent ethylene for 1 hour, 0.1 percent ethylene chlorhydrin in water for 45 minutes, ethylene chlorhydrin vapor for 50 minutes, ether vapor for 45 minutes, or 2 percent sucrose in water for 24 hours. At that time branches kept in tap water required about 12 days to flower. The sugar treatment hastened flowering by 2 or 3 days in 5 species. Other treatments did not hasten--or inhibited--flowering.

Pollen of Acer platanoides, A. saccharum, A. nigrum, and A. negundo that was stored for as long as 8, 16, 17, and 25 days respectively gave at least some seed set when used in intra-specific pollinations. No longer trials were made. Pollen of A. platanoides could be satisfactorily stored for at least 8 days by keeping cut branches in water in the refrigerator and removing the flowers as needed.

In general, little difficulty was encountered in hastening flowering or storing pollen for the few days that were needed in order to match the blooming periods of most species-pairs. It was only in trying to use the late species on the very early-blooming silver maple that the difficulty was serious.

Pollen collection from A. platanoides and its close relatives and A. henryi was difficult. These species shed very little pollen and an hour's collection could hardly be seen in the bottom of a vial. In 1947 and 1948, when collected pollen was used, seed sets were very low in crosses involving these species as male parents. This was probably due to lack of pollination, since it was usually impossible to be sure that every stigma received pollen. In 1949 and 1950 freshly opened anthers were used as pollinating brushes and seed sets were much higher.

Pollinated & Unpollinated Samaras

In the spring-fruiting red maple, fruits of unpollinated and unsuccessfully pollinated flowers enlarged little or none and dropped about 4 weeks after pollination. Fruits of successfully pollinated flowers started to enlarge shortly before this flower drop and showed little mortality thereafter.

In the fall-fruiting A. platanoides and A. palmatum, fruits from all flowers enlarged to about half size within 2 to 4 weeks of pollination. Soon thereafter the unpollinated or unsuccessfully pollinated fruits dropped and successfully pollinated fruits enlarged rapidly with little subsequent loss. The similarity of behavior of unpollinated and unsuccessfully pollinated fruits indicates that in wide crosses fertilization did not take place or abortion occurred very early. None of these species is parthenocarpic.

A. negundo is nearly 100 percent vegetatively parthenocarpic and pinch tests at fruit maturity were necessary to determine which pollinations were successful. Limited data indicate that A. buergerianum and A. saccharum may also be parthenocarpic.

In A. platanoides but not in other species it was noted that the seeds resulting from certain interspecific combinations were much smaller than were any of the seeds resulting from intraspecific pollinations (table 1). These small seeds ripened earlier than did normal seeds, and had much smaller cotyledons. The embryos were alive at the end of the stratification period but did not germinate (A. platanoides x saccharum) or gave weak seedlings (A. platanoides x mayrii). Presumably they might be propagated successfully by embryo culture if excised in July or August.

TABLE 1.--Relative weight of seed from crosses on Acer platanoides female parents, 1950*

Male parent	Number of seeds	Relative seed weight
A. platanoides	296	100
Self	22	103
A. cappadocicum	69	103
A. mayrii	75	64
A. saccharum	92	35

*Embryo plus seed coat.

In all species, both members of a samara pair may contain filled seeds.

Controlled Pollinations

With few exceptions seed sets to open and intraspecific pollinations were high. The exceptions are:

A. saccharinum.--This species usually flowered long before cold weather was past and consequently lost most of its flower crop.

A. platanoides, 1948.--In this year only, several flowering trees failed to fruit.

A. rubrum.--One tree of this normally fruitful species has produced many female flowers but no fruit in each of 5 years. This may be due to genetic causes.

Crosses between species in the same section of the genus were moderately and consistently successful. But most of the crosses between species in different sections of the genus only one (Platanoides x saccharum and reciprocal) was successful (table 2).

TABLE 2.--Summary of results of maple (Acer) breeding, 1947-50

Female parent	Unpollinated control	Male parent											
		Platanoidea				Saccharina		Palmata		Rubra		Negundo	
		Self	platanoides	mayrii	cappadocicum	saccharum	nigrum	palmatum	japonicum	rubrum	saccharinum	henryi	negundo
platanoides	640 0	231 4.8	2,210 26.3	1,686 5.2	1,244 9.2	3,266 1.8			269 0	709 0.2	96 0	69 0	1,500 0.4
saccharum	109 **	49 4.0	220 4.1			106 46.0	241 8.9			208 **	59 0		88 0.6
buergerianum	80 0							58 **					
palmatum	200 0		128 0			43 0		40 27.6	50 0				32 0
rubrum*	4,300 0.09	100 1.9	180 0	280 0	1,600 0	780 0				22,000 18.5	2,240 19.3		4,550 0
saccharinum*										450 5.1			
negundo*	1,000 0.1		2,100 1.1			6,900 0.6	140 0.7			1,600 1.3	380 0.5	2,600 5.2	4,600 33.4

*Number of flowers was calculated on the basis of 4 per inflorescence in *A. rubrum* and *A. saccharinum*, 6 in *A. negundo*.

**Normal samaras matured but were probably empty; hardness of pericarp made pinch test difficult. No seed germinated.

Legend: 250 / 4.2 — Number of flowers pollinated. Percent of ovules maturing filled seed.

Shading in corners indicates hybridization successful, as judged by seed set and seedling appearance.

The strong genetic barriers to crossability between distantly related species have presumably arisen through the accumulation of many small mutations, translocations, or inversions. Differences in chromosome number cannot account for the lack of seed set, for most of the failures involved diploid species. A. saccharinum is tetraploid or possibly hexaploid in part; A. rubrum is hexaploid and octoploid;

A. platanoides is diploid or possibly tetraploid in part; all the other species used are diploid (9, 13, 38).

Variation in species crossability among different trees of the same species is shown in table 3, in which are included all trees of two species that were used as female parents for the same cross in two different years. Trees that were good producers of one type of hybrid seed in one year were also good producers of the same type of seed the next year. But trees that were good producers of one type of hybrid seed were not necessarily good producers of other types.

TABLE 3.--Seed set of maple in different years on the same female parent

Female parent	Year	Male parent					
		platanoides	*cappadocicum*	*mayrii*	*saccharum*	*negundo*	*henryi*
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
A. platanoides:							
G-608	1949	16.0	0.5	0.6	1.4	--	--
	1950	20.0	7.7	0	6.2	--	--
G-610	1949	31.2	0	1.5	5.1	--	--
	1950	55.5	4.6	--	21.2	--	--
G-632	1948	14.2	--	--	0	--	--
	1950	55.5	1.2	13.6	1.0	--	--
G-1916	1949	43.7	26.2	7.4	0.5	--	--
	1950	39.0	16.8	17.8	1.9	--	--
A. negundo:							
G-581	1949	--	--	--	--	50.6	2.8
	1950	--	--	--	--	60.6	0.1
G-594	1949	--	--	--	--	46.5	16.7
	1950	--	--	--	--	71.5	22.2

Table 4 contains a summary of all known maple crosses. Most are intrasectional, as were the hybrids produced in our experiments. However, Rehder lists a number of natural intersectional hybrids (27). Most of these are rare and presumably resulted from the cross-pollination of hundreds or thousands of flowers. Albenski, however, reports several successful artificial hybrids between sections, with supporting growth data for some of them (1).

TABLE 4.--Summary of reported crosses in the genus Acer

Female parent	Male parent: Platanoidea				Campestria		Saccharina			Spicata		Palmata		Rubra		Negundo	
	platanoides	*mayrii*	*cappadocicum*	*lobelii*	*campestre*	*monspessulanum*	*saccharum*	*nigrum*	*leucoderme*	*pseudoplatanus*	*tataricum*	*palmatum*	*japonicum*	*rubrum*	*saccharinum*	*henryi*	*negundo*
platanoides	H 9,10	H 10	H 9,10	H* 6			F 9 H 10					F 9	F 10	U 9 F 10	F 10	F 10	H 1 U 9 F 10
lobelii	H* 6																
campestre					H 9	H* 6				H* 6							
monspessulanum					H* 6					H* 6	H* 6						
opalus						H* 6											
saccharum	H 10		F 9		F 9		H 9,10	H 2,3,4	H 4,8,10			U 9		F 9,10	U 9 F 10		U 9,10
nigrum							H* 2,3,4										
leucoderme							H 4,8										
pseudoplatanus					H* 6	H* 6											
buergerianum												F 10					
tataricum	H 1				H 1	H* 6											H 1
palmatum	F 10						F 10					H 9,10	F 10				F 10
pennsylvanicum (Macrantha)											H* 6						
rubrum	F 9,10	F 10	F 9,10		F 9		F 9,10					F 9		H 9,10	H 5,7,9 10		F 10
saccharinum														H 9,10	H 9		
negundo	H 1 U 10						F 10	F 10						F 10	H 1 F 10	H 10	H 10

*Direction of cross unknown.

Legend:
H -- Hybrids obtained
U -- Undetermined; possibly hybrids
F -- Failure

Authorities:

1. Albenski (1)
2. Anderson and Hubricht (2)
3. Dansereau and Lafond (7)
4. Desmerais (8)
5. Freeman (14)
6. Rehder (27)
7. Sax, Karl (unpublished)
8. Slavin (37)
9. Northeast. Forest Expt. Sta. (unpublished data, 1927-41)
10. Author's studies

Criteria Of Hybridity

The following notes give the macroscopic differences observed in the first 1, 2, or 3 years in those lots believed to be true or probable hybrids:

A. platanoides x mayrii.--Hybridity certain. Seeds were set in 8 out of 12 crosses, and were usually smaller than were nonhybrid seed from the same female parent (table 1); seeds germinated faster than did nonhybrid seeds (table 5); cotyledons were wider, longer and darker green on hybrids than on nonhybrids; foliage and height of 1-year old seedlings were not distinctive; many hybrids of the 1950 crop died soon after germination.

TABLE 5.--Average germination time for Acer seed from 1949 controlled pollinations

Combination	Mean germination time	Standard error
	Days	*Days*
platanoides x platanoides	24.4	± 1.2
platanoides x saccharum	6.5	± 4.1
platanoides x mayrii	9.1	± 1.2
platanoides x cappadocicum	13.1	± 1.7
negundo x negundo	14.0	± 0.4
negundo x henryi	16.2	± 1.0

A. platanoides x cappadocicum.--Hybridity certain. Seeds were set in 9 out of 10 crosses and were often larger than nonhybrid seeds; seeds germinated more quickly than nonhybrid seeds; cotyledons were larger than on nonhybrids; first-year seedlings outgrew nonhybrids by about 25 percent and leaves had many cappadocicum characters.

A. platanoides x saccharum.--Hybridity certain. Seeds were set in 11 out of 34 crosses; most of seeds were very poorly developed, but did contain an embryo. The few seeds that germinated were of nearly normal size and germinated more quickly than did nonhybrid seeds. The seedlings obtained resembled straight A. platanoides, but are slightly smaller and darker green.

A. saccharum x platanoides.--Hybridity probable. Seeds set in two out of five crosses, possibly as a result of selfing. Seedlings had nearly unlobed leaves that did

not resemble A. saccharum in shape, but did in texture.

A. saccharum x nigrum.--Hybridity certain. Seeds were set in all bags in two out of two crosses; seeds germinated slightly slower than nonhybrid seeds. There were no growth differences the first year. This may represent a backcross, as the male parent had some sugar maple characters.

A. rubrum x saccharinum.--Hybridity certain. Reports by other workers and high seed sets leave no doubts as to hybridity.

A. negundo x henryi.--Hybridity certain. Crosses were unsuccessful during the first 2 years, but very successful in 1949 and 1950. Hybrid seeds germinated slightly slower than nonhybrid seeds. Hybrid seedlings were distinguishable from cotyledon stage onward by more regular leaf-lobing, pronounced red color of the young leaves, and about 25 percent greater growth in height.

Two of the successful crosses look promising on the basis of 2 years' performance. The seedlings of A. negundo x henryi grew considerably faster than did nonhybrid seedlings from the same female parent, although not so fast as did seedlings from other A. negundo females. Young leaves were brightly colored, becoming apple-green with a tinge of red when mature; on young seedlings at least there is pleasing red growth throughout the summer. The hybrids may prove useful for windbreak or ornamental plantings, but are probably not suited for timber production.

The other promising cross is A. platanoides x cappadocicum. The first species is a highly esteemed producer of quality lumber in Europe and is widely adapted in this country, becoming naturalized in many stands in the Philadelphia area, where it has good form when grown in closed stands. No information is available about the wood quality or timber form of the second species. The hybrid seedlings grew rapidly.

Discussion

Interspecific hybridization, especially between closely related species, seems to be a fruitful line of attack for maple improvement. Some crosses are easily made and some of the resulting hybrids grow fast.

But mass-production of the hybrids by seed is a stumbling block. With artificial methods the seed produc-

tion per man-day is very small. Nor is it likely that natural crossing gardens will do much better. Most of the crossable species bloom at different times. Too, as Grant (15) has emphasized, differences in flower structure are very effective isolating mechanisms in insect-pollinated plants--and especially so in plants pollinated by honeybees. The maples are honeybee-pollinated and exhibit a wide diversity in flower structure; so they may not cross easily when interplanted.

Making the hybrids true-breeding by doubling their chromosome numbers with colchicine seems to offer a possible way of achieving mass-production. Of course, we know nothing yet as to whether the doubling will in itself be detrimental. Selection and hybridization within species are also promising and will not involve the same difficulties in mass-producing the seed.

FRAXINUS

Two types of pollination bags were used--sausage casings and vegetable parchment. In 1947 the sausage casings offered nearly complete protection against a heavy late frost; the vegetable parchment did not. In 1950 comparative tests of the two types of bags were made. On Fraxinus excelsior both bags gave heavy fruit set but on F. pennsylvanica the sausage casings were greatly superior to the vegetable parchment.

Fruit set of F. excelsior to intraspecific pollination was stimulated in 1950 and 1951 by bagging (with either type of bag) for a 3-week period immediately following pollination. Bagged branches gave seed sets 15 times greater than did hand-pollinated branches that were not bagged.

In 1950 branches of F. pennsylvanica (pollinated by F. velutina) that were bagged continuously from pollination until fruit maturity with sausage casings gave a very heavy crop of empty samaras. In 1951 similarly treated branches matured very heavy crops (300 or more samaras per branchlet) of filled, unweeviled samaras.

The pollination bags react adversely on young leaves, killing them if left on too long. They hasten flowering but delay stigmatic withering by a few days and (in F. excelsior) hasten the early development of the fruit by a week or more. It is possible that all these effects--as well as the increased yields of samaras per branch--are due to the maintenance of higher temperatures during the weeks following pollination.

The seed sets of F. americana and F. pennsylvanica did not differ between the earliest pollinations (made when the panicles were just issuing from the bud and the pistils were 1 mm. long) and later pollinations (made when the panicles were 5-8 cm. long and the styles were up to 8 mm. long) as long as the stigmas were all in a fresh condition. However, pollinations made after any of the stigmas on the tree started to wither were nearly complete failures.

In all years seed weeviling was severe in green and white ash. Cloth bagging in mid-July (1950), but not in late August (1947-49), gave practically complete weevil control.

Controlled Pollinations

In nearly all cases, intraspecific pollination gave somewhat higher seed sets than were obtained from open pollination (table 6). The failures were due to pollination in an off-year or to pollination after the receptive period was passed. There was no evidence of incompatibilities within species.

TABLE 6.--Summary of results of ash (Fraxinus) breeding, 1947-50

Female parent	Wind	Unpollinated control*	Male parent: Melioides: *americana*	Melioides: *pennsylvanica*	Melioides: *velutina*	Bumelioides: *excelsior*	Bumelioides: *quadrangulata*
americana	Many 0-50 --	217 0.1 --	387* 5.6 95	859* 0.1 0.5	34* 0 0	21* 0.9 2	
pennsylvanica	Many 0-50 --	62 0 --	687 0.1 1.1	497 6.3 50	272 7.7 35	20 0 0	
velutina	Many 0-50 --	6 0 --		96 10.4 15	16 10.4 11		
excelsior	Many 1 --	35 0.1** --		33 0.6** 0.6		157 16.7 50	9 0.5** 0.5

*Assuming 100 flowers per panicle in Melioides, 50 in *F. excelsior*.
**Matured seeds are probably the result of selfing.

Legend:

25	Number of flowers pollinated, in hundreds (estimated).
2.3	Average seed set, in percent (estimated).
50	Highest seed set obtained, in percent (estimated).

Shading in corners indicates pollination was apparently successful, judging by comparative seed set or appearance of progeny.

Both the pubescent (var. typica) and glabrous (var. lanceolata) varieties of F. pennsylvanica were used. They were interfertile and reacted similarly when crossed with other species. This was expected since they are not well separated geographically and appear to belong to the same breeding population.

Except in F. excelsior, fertilized and unfertilized samaras grew at the same rate for about 3 weeks after pollination. At this time they were about 3 mm. long. The unfertilized fruits grew little after that and soon dropped, whereas fertilized fruits attained full size by the sixth week. By the fifth week unfertilized fruits were 6-12 mm. long and dropping; fertilized fruits were full size (20-30 mm. long). In all species there was little mortality among fertilized fruits after the sixth week.

There was no evidence of vegetative parthenocarpy.

Of nine different interspecific combinations tried, only two were certainly successful: F. pennsylvanica x. velutina and reciprocal. The few seeds matured to other crosses were probably the result of selfing (on F. excelsior female) or of contamination.

The hybridity of the F. pennsylvanica x velutina and reciprocal seedlings is attested by:

1. Consistently high seed sets for different trees and different years.

2. The occurrence in the progeny from the 1948 crosses of 0/98 albinos from F. velutina x pennsylvanica and of 3/11 albinos from the intraspecific cross (probably between siblings) in F. velutina. The female parent was the same in both cases. (With a chi-square value of 25.3 and 1 d.f. this difference is significant.)

3. The two species are much more closely related taxonomically than are any of the other species-pairs considered. They differ in many slight quantitative characters.

To date no significant differences have been found in growth performance or appearance between hybrid and non-hybrid progeny from the same female.

Polyploidy is known in the genus. It was thought that differences in chromosome number might be responsible for the lack of crossing in some cases. Accordingly stomata measurements were made of the F. americana parents and root-

tip counts were made on F. velutina from several origins to supplement earlier counts (31, 41). All the F. americana parents used were diploid and no polyploids have been found in the other species. Hence lack of crossability seems due to genic differentiation, translocations, etc. rather than to differences in chromosome number.

Previous Hybridizations

The following hybrids have been reported previously:
F. richardi x americana
F. richardi x pennsylvanica
F. excelsior var. aureovariegata x americana
F. excelsior var. aureovariegata x pennsylvanica
F. excelsior var. aureovariegata x quadrangulata
F. oxycarpa x pallisae
The first five are artificial hybrids made by Johnson and Heimburger (19); the last is a hybrid described by Anderson and Turrill (3).

Our findings are at variance with those of Johnson and Heimburger. They report rather high seed sets from crosses involving species in different subsections, and between F. richardi (= F. pennsylvanica?), F. pennsylvanica, and F. americana. The crosses we attempted failed to take unless they were between very closely related species; even the cross F. pennsylvanica x americana failed even though the species are in the same subsection and are often misidentified in the field.

Discussion

Lack of flowering material and the inability of many female trees to mature fruit after pollination (at least in certain years) are the major hindrances to controlled-pollination experiments in ash. Five years' fruiting observations indicate that an ash-breeding arboretum should contain 10 to 20 or more trees per biotype to make up for the lack of flowering and fruiting.

Some 15 species have been grown for 20 years or more in this area. From casual observations, the two common natives (F. americana and F. pennsylvanica) grow up to twice as fast as the best exotic (F. excelsior). However, some of the western American species are showing up well in nursery trials. In view of the relative lack of species crossability, future improvement work in this area should stress selection within these two species and hybridization within species and with their very close western American relatives.

LIRIODENDRON

Carpenter and Guard (5) have described techniques used in controlled-pollination experiments in yellow-poplar (tuliptree). The techniques we used were similar to theirs in these respects: Bud stage chosen for working, freshness of pollen used, pollination immediately after emasculation, and length of stratification period. Our techniques differed from theirs as follows: We used sausage-casing bags instead of Kraft-paper bags, pollen from freshly opened anthers instead of from unopened anthers, removed the perianth completely in performing emasculations, shipped flower buds via ordinary mail rather than air mail although packed in the same way, and judged seed filling from germination behavior rather than from cutting tests.

In various years some of the flowers have been emasculated and bagged but not pollinated. These tests indicate that the species is almost completely vegetatively parthenocarpic, as there were no differences between pollinated and unpollinated flowers in the percentage of flowers developing normal-sized seed. This is shown in the following tabulation, which includes all pollinations made.

Treatment, all flowers emasculated and bagged	Flowers treated	Flowers maturing normal fruit
Not pollinated	35	32
Pollinated	347	318

To determine in what portion of the flowering season the flowers are most receptive, pollinations were made at intervals in 1950. Pollinations made when 1 to 10, 25, 50, and 75 percent of the flowers on the trees had reached anthesis gave 8, 11, 5, and 7 percent germinable seed respectively. There seems to be no clearly defined superiority of early over late pollinations.

Another series of pollinations was made to determine the correct stage of bud development to choose for emasculation and pollination (table 7). There seems to be a wide latitude in choice of buds.

Liriodendron is insect-pollinated. Flies, beetles, honeybees, and bumblebees in decreasing order of abundance were observed on the opened flowers, whether emasculated or not. The number of insect visitors always seemed sufficient to insure the pollination of all stigmas. A great deal of selfing seemed to take place, because insects were often

seen traveling from anther to stigma of the same flower.

The results of all pollinations are given in table 8. In all cases the female parents were native Philadelphia trees. One female parent (G-1645) was superior as a producer of filled seeds after almost all types of pollination. No single male parent showed such superiority. In most cases the males that gave high yields on one female parent gave very low yields on other female trees. And (aside from G-1645) the female giving the highest yield with one male was not the same for other males. This suggests that there was interaction between male and female although differences in seed yield due to time of day of pollination, condition of pollen, etc., are not ruled out. It is not known whether

TABLE 7.--Germinable Liriodendron seed obtained after pollination at various stages of bud development, 1950

Stage of bud development	Germinable seeds from cross--		
	G-1640 x G-754	G-1640 x G-755	G-1645 x G-754
	Percent	*Percent*	*Percent*
Buds hard, bracts tight	--	--	36
Buds slightly soft, bracts dropped	7	11	19
Buds very soft	3	5	62
Buds slightly open, pollen yet unshed	1	3	51

*TABLE 8.--Yields of germinable seed obtained from intraspecific crosses of Liriodendron tulipifera, 1947-50**

Female parent	Approximate percentage of filled seeds after pollination by--			
	Insects (flowers unbagged)	Self	Pollen from** 1 to 3 other nearby trees	Pollen from** 1 to 14 trees from Pa., Ind., Ohio, and Va.
G-754	1	1	0-1	0-18
G-755	3	0	6	0-11
G-1640	1	0	1-5	0-13
G-1645	9	11	40	1-26
M813	1	0	5	0- 8

*Percentages are based on the number of germinable seeds obtained from the fruits of 3 to 9 matured flowers per pollination (25 to 100 flowers for the yields after open pollination). Each flower is assumed to have 85 carpels.

**The pollens and resulting seedlings were kept separate according to male parent tree.

the low degree of selfing and these interactions mean the presence of genetic incompatibilities. They might be explained equally well by A. G. Johnson's observation (personal communication) of meiotic irregularities in this species.

Observation of pollinating insects indicated that pollination by self or by nearby closely related trees might explain the small amount of sound seed usually found in yellow-poplar after open pollination. The crossing data do not support this conclusion, for the yields after open pollination are about what might be expected after pollination by a random group of either nearby or distant trees.

The percentages of good seed were much lower than were obtained by Carpenter and Guard, who reported a range of 0 to 5.6 percent after selfing, 2.4 to 34.8 percent after open pollination, and 28 to 90 percent after crossing. Differences in methods of determining sound seed and in pollination technique no doubt account for some of the superiority of their results. Differences in seed-setting ability of females in the two localities probably played a part, too.

To date no significant differences in growth of the progenies have been noted. However, all the selfed and most of the crossed progenies are only 1 year old.

QUERCUS

Piatnitsky (24) has reported that vegetable parchment bags are better for the oaks than are Kraft paper or sausage casing. Accordingly, they were used exclusively. They caused a little leaf damage when left on too long, but no apparent flower damage. However, seed sets on the best bagged branches were considerably lower than on open-pollinated branches on the same trees.

W. S. Flory, Jr., (personal communication) practiced selection for fruitfulness in duplicating the original Ness hybrids. He worked only trees that showed their ability to mature fruit by having a good crop of year-old acorns in addition to flowers at the time the pollinations were made. The present data confirm the need for such selection, since the controlled pollinations were successful on four trees that matured heavy acorn crops but were failures on eight trees that matured no acorns to open pollination the same year.

Piatnitsky (26) reported that oak stigmas are receptive for a week or more, i.e., during the entire period during which there is no apparent external change in the stigmas. To check this, the 1947 pollinations were made at intervals. The results confirmed Piatnitsky's conclusion, for seeds were obtained from pollinations made at all stages.

In late July 1947, heavily fruiting branches on several trees were sprayed with 10 and 30 ppm. naphthaleneacetic acid and 25 ppm. 2,4-dichlorophenoxyacetic acid in an attempt to increase fruit set. At the end of September of the same year there were no significant differences between treated and untreated branches in mortality of either first- or second-year acorns.

TABLE 9.--Summary of results of oak (Quercus) breeding, 1947-48

Female parent	Wind	Unpollinated control	Male parent: Self	velutina	borealis var. maxima	robur	alba
velutina (1 tree)	Many 1,000+ --	117 0 --		174 2 0	139 11 6		
borealis var. maxima (2 trees)	Many 1,000+ --	109 0 --	123 0 --	357 8 6	307 34 23		
alba (2 trees)	Many 1,000+ --	86 0 --	18 0 --			1,052 2 0	291 13 2

*Data for 8 trees that set no seed to wind pollination or controlled pollination are omitted.

Legend:

357	Flowers pollinated.
8	Acorns matured.
6	Acorns germinated.

Shading in corners indicates presumably successful combination.

The crosses made are listed in table 9. The one cross known to be successful was Quercus borealis var. maxima x velutina and reciprocal. The progeny of this cross have leaves that are broader and less deeply lobed than are leaves of seedlings of the female parent. The leaves of the reciprocal hybrids are similar to those of seedlings of the

male parent. The hybrids are smaller than are red oak seedlings from the same parents. When grown in the nursery in close proximity to nonhybrids, the hybrids were fairly easy to recognize in their first, second, and third years. Presumably they could be easily recognized if grown on a mass-production basis, but not necessarily in the wild. Several putative natural hybrids of this cross (x Q. hawkinsii Sudworth) have been found (23).

The following artificial hybrids have been reported in the oaks:

Q. virginia x lyrata (12, 22).
Q. robur x borealis var. maxima (25).
Q. robur x macranthera (25).
Q. robur x macrocarpa (25).
Q. macranthera x robur (25).
Q. macranthera x borealis var. maxima (25).
Q. macrocarpa x borealis var. maxima (25).
Q. alba x robur (35).

In addition numerous natural hybrids are known (23).

ABIES

Limited crossing of firs was attempted in 1947 and 1948, using single specimens of Abies veitchii, A. homolepis, A. cephalonica var. apollininis, A. nordmanniana, and A. concolor as females and these same trees plus A. lasiocarpa as males.

The flowering branches were enclosed in sausage casings when the female flowers were halfway out of the bud and the scales were still closed or had just started to open. The flowers are brittle and easily broken at this stage. The bags were left on until about 2 weeks after pollination; they caused some needle burning but little cone loss.

Cone loss varied from 0 to 100 percent. This loss was apparently not related to pollination, bagging, nor to any obvious environmental factor. The cone-set data, grouped for all species, are given below:

Bagging and pollination treatment	Flowers treated	Cones matured
Unbagged, pollinated by wind	230	99
Bagged, unpollinated	20	13
Bagged and selfed or crossed	191	60

Not only are the firs parthenocarpic, but unpollinated cones contained nearly a full complement of full-size seeds. This made it impossible to judge success of the pollinations from the seed-set data. Germination was erratic and low, due either to poor seed filling or to poor technique; and no conclusions as to species crossability are possible. (It has since been found that 4 months' stratification gives nearly 100 percent germination and that pinch tests of soaked seeds can be used to test seed filling.)

In 1949, collections of wind-pollinated seed were made from isolated trees of A. cephalonica, A. nordmanniana, and A. cilicica in the hope of obtaining natural hybrids. All the trees were subject to cross-pollination by other species. The percentage of sound seeds varied from 3 to 10 percent. The resultant seedlings were uniform in appearance, suggesting that the seeds were from selfing and that no natural hybridization had taken place.

Previously reported hybrids in the genus are:

A. pinsapo x cephalonica and reciprocal. Natural, raised in 1868 (27).
A. pinsapo x nordmanniana and reciprocal. Natural, raised in 1872 (27).
A. nordmanniana x cilicica. Artificial (16).
A. nordmanniana x cephalonica. Artificial (16).
A. lowiana x grandis. Artificial (20).
A. sibirica x veitchii olivacea. Artificial (11).

PICEA

Sausage casing bags were used. These caused considerable needle loss on white spruce but had little effect on cone or seed set.

Much of the bagging had to be done after the female flower buds had opened, but usually before noticeable pollen shedding. In spite of the late bagging nearly all unpollinated controls gave no seeds.

In most species the cone scales are partially or fully open as soon as the flowers emerge from the bud and they remain in this condition for 2 or 3 days or longer in some years. Pollen shedding on the same tree occurs during this period or at least overlaps it considerably. It is difficult to recognize stages of flower opening within this period. (In Picea abies however, stages may be recognized, since the flowers enlarge three- or four-fold and the bud scales open more before closing.)

Accordingly, in 1950 pollinations were made during each of the two stages that may be recognized in P. glauca: (1) a stage in which most of the flowers on the tree still retained a "cap" of bud scales, and (2) a stage in which this "cap" had dropped. For the "cap-on" stage the seed sets were 0.3, 0.7, 1.0, and 2.9 good seeds per cone for

TABLE 10.--Summary of results of spruce (Picea) breeding, 1948-51

Female parent	Wind	Unpollinated control	Male parent: Self	Wilsonii	Maximowiczi	asperata	abies	glauca	Likiangensis	montigena
BRANCHES BAGGED BEFORE AND AFTER POLLINATION										
abies	15 40 5.0	3 0.3 0	4 32 0.5			9 193 14		6 27 0		
mariana	7 0 0	7 0 0				30 1.3 0	17 0.5 0	17 3.4 0		
glauca	173 25 0.8	31 0.07 0	6 12 1.3			190 2.7 0	17 0.4 0	86 4.5 1.1		
omorika	24 0.2 0					8 0.1 0	1 1.0 0			
FLOWERS SUBJECT TO WIND POLLINATION *Recorded seed sets include only those seeds set in excess of amount expected from wind pollination alone*										
asperata	611 ca.50 5.1		35 ca.50 1.8		2 150 12*	1 44 172*	140 50 16	5 180 17*		
abies	58 81 4.3		2 30 0		1 15 1.0	91 350 7.5	6 0 18	3 0 0		7 0 0.5
mariana	45 1.2 0						66 2.1 0	60 8.2 0	59 2.8 0	
glauca	992 1.7 0.17		47 14 1.2	185 2.6 0.06	66 10 0.18	285 8.9 0.03	140 5.6 0.12	346 3.0 3.7	197 7.7 0.04	43 2.9 0.09
montigena	52 85 1.7					20 0 29	73 0 5.0	19 0 1.1		
omorika	62 1.0 0.5			56 0.5 0.3					68 1.5 0.2	

*There were no open-pollinated cones on these trees; so it was inadvisable to make judgment as to probable hybridity of the seeds. The cross *asperata x asperata* was made in quantity on another tree but all the cones so crossed were cut early by squirrels, indicating a high content of good seeds.

Legend:

185	Number of cones matured.
2.6	Number of empty seeds per cone.
0.3	Number of filled seeds per cone.

Shading in corners indicates apparently successful pollination.

4 different trees. For the "caps-off" stage the seed sets were 1.4, 1.6, 2.3, 3.2, and 5.2 good seeds per cone for 5 other trees. Although inconclusive, the results indicate an advantage of late pollination.

All species tested (except possibly P. omorika) proved to be practically 100 percent vegetatively parthenocarpic. Thus in table 10 only the number of cones matured is given, as this is nearly the same as the number of flowers pollinated.

Seed sets to open pollination were moderate in P. abies and P. asperata, very low in other species (table 10). This is a consequence of the small amount of pollen produced: these two species produce moderate amounts, and the other species very little.

There are additional data for nine trees of P. montigena, P. omorika, P. orientalis, and P. polita not included in table 10. For 13 crops from these trees the maximum yield to open pollination was 2.0 good seeds per cone; 8 of the crops gave no good seed.

Controlled Pollinations

The crosses made are summarized in table 10. In P. glauca some of the trees set as much seed to selfing as to crossing; others set no seed to selfing. The one tree tested in P. abies was slightly self-compatible.

Nearly all crosses attempted resulted in some normal-sized empty seeds. Except for P. glauca x glauca (which may have been insufficiently pollinated) the number of empty seed was greatest for the crosses also giving full seeds, indicating that the presence of many empty seeds means greater possibility of ultimate success.

Of 30 interspecific combinations tried, 3 were apparently successful--P. abies x asperata and reciprocal, P. montigena x asperata, and P. montigena x abies. Probable hybridity must as yet be judged solely by the consistency and size of the seed sets. These crosses were moderately to highly successful each time tried.

There are as yet no data on the growth performance of the hybrids. A priori reasoning indicates that the cross P. asperata x abies and reciprocal is promising. Norway spruce has already proved itself, and Teng (39) regards P. asperata as the most widespread and promising for dry climates of all the Chinese spruces. Its wood is used for

general construction but is lighter than that of most other spruces. Apparently the species is very variable, and new germ plasm is needed, because the only flowering specimens

TABLE 11.--Summary of reported crosses in the genus Picea

Female parent	Male parent: Eupicea									Casicta						Omorika	
	wilsonii	*maximowiczii*	*asperata*	*abies*	*orientalis*	*obovata*	*rubens*	*mariana*	*glauca*	*engelmanni*	*pungens*	*likiangensis*	*montigena*	*jezoensis*	*sitchensis*	*omorika*	*breweriana*
asperata		U 6	H 6	H 6		H 1			U 6								
abies		F 6	H 6	H 6	U 5		H 3	H 3	H 3 U 5 F 6				F 6				
orientalis				F 5					F 5								
rubens				H 3				H 3									
mariana			F 6	F 6 H 3			H 3		H 3 F 6			F 6		H* 4			
glauca	F 6	F 6	F 6	H 3 F 5,6	U 5		H 3	H 3	H 5,6	H* 1,2	H 3	F 6	F 6	H* 4	H* 1,2		
glehnii														H* 4			
montigena			H 6	H 6					F 6								
sitchensis										H* 2						H 1	
omorika	F 6		F 1,6	F 6		F* 1			F 6			F 6					F* 1

*Direction of cross unknown.

Legend:
H -- Hybrids obtained
U -- Undetermined; possible hybrids
F -- Failure

Authorities:
1. Eklundh (11)
2. Johnson (17)
3. Johnson and Heimburger (19)
4. Rehder (27)
5. Northeast. Forest Expt. Sta. (unpublished data, 1937-41
6. Author's studies

in Philadelphia are too broad-crowned and coarse-branched (at least in the open) to be used as a timber type. The two species are considered as closely related by Rehder (27).

Previous Work

In table 11 the crosses made by previous workers are summarized in addition to the crosses reported here.

The crossability pattern indicated by the data of Johnson and Heimburger (19) is far different from that indicated by our data. They report high seed sets from practically every cross attempted, whereas most of ours were complete or near failures. For four crosses there is a definite contradiction between the two sets of data.

The natural hybrids reported by Rehder (27) are presumably the result of rare crosses and may or may not give high seed sets artificially. Apparently all the crosses reported as successful by Eklundh (11) gave moderate to high seed sets.

There is little or no correlation between taxonomic position and ease of hybridization.

PINUS

Cone mortality on individual trees varied from 0 to nearly 100 percent. Most of it occurred the first year or early in the second growing season. Rarely was there much mortality in the 2 or 3 months preceeding cone ripening, although earlier weevil damage frequently became evident then.

Much of this mortality is attributable to the following factors: (1) insect damage to the flower buds or young flowers, (2) weevil damage to near-mature cones, (3) continuing internal (genetic?) factors within the tree, (4) previous heavy cone crop, (5) lack of proper pollination, and (6) bagging treatment. Strangely, few cones were lost to squirrels in spite of a heavy squirrel population.

In P. densiflora, P. resinosa, and P. nigra in 1948 and in P. griffithii in 1951 there was almost total flower mortality on some trees due to insects present in the flowering shoots prior to bagging. In P. strobus, P. griffithii, and P. flexilis especially there was always light to moderate mortality from cone weevils.

We suspect that genetic factors are involved in the consistently heavy cone mortality of certain vigorous P. strobus trees.

It is probable that the relatively poor cone crops on some large P. griffithii and on most P. resinosa from 1947 to 1950 were due to depletion of food reserves by a previous heavy cone crop. Similarly the heavy cone crops from 1947 to 1950 on many P. strobus trees probably influenced the heavy cone mortality of the 1950-51 crop.

Pollination was necessary for normal cone development in most species; only P. griffithii, one tree of P. rigida, and several trees of P. strobus were vegetatively parthenocarpic. In the five-needled white pines, pollination by any other five-needled species (but not by the three-needled soft pine P. bungeana or by various hard pines) resulted in the development of normal cones. In the series Lariciones, pollination by nearly any other member of the series resulted in the development of normal cones containing empty or full seeds. There are seven exceptions, as follows:

Female parent	Male parent	Results
P. parviflora	P. griffithii	Few very small cones.
P. resinosa	P. tabulaeformis	No cones.
P. densiflora	P. tabulaeformis	Many small cones, no seeds.
P. sylvestris	P. tabulaeformis	Few small cones, no seeds.
P. sylvestris	P. taiwanensis	No cones.
P. nigra	P. tabulaeformis	Few cones, few seeds.
P. tabulaeformis	P. massoniana	Few cones, no seeds.

In P. parviflora there is a peculiar relation between fertilization and cone size. The seeds are large in relation to the mass of the cone, and a fully developed seed causes a bulge in the subtending cone scale, making it possible to estimate the number of seeds in unopened cones.

In several trees of P. strobus intraspecific crossing resulted in significantly lower cone set than did interspecific crossing.

In general, type of bag used--vegetable parchment or sausage casing--had little effect on cone set. However, for P. griffithii the vegetable parchment bags were found to be definitely inferior--perhaps by affecting stage of flower development and hence whether or not the pollinations were effective. A priori, leaving of the pollination bags on until maturity would seem detrimental to cone set. However, there were a few accidental cases in which continuous bagging did no harm and may have benefited cone and seed set (42).

Seed Sets To Wind Pollination

Seed sets to wind-pollination for the trees used in the control-pollination work are given in tables 14 and 17. They are low for most species. For P. flexilis, P. parviflora, P. strobus, and P. sylvestris the seed sets shown are typical of nearly all trees in the Philadelphia area and are a consequence of the small amount of pollen produced; even trees planted in groups of 10 or 20 are not adequately pollinated.

It is possible to work most trees of these species without bagging if the expected seed set is reasonably high. In 1949-50 this was done on one tree, from which 89 P. strobus x griffithii and 78 P. strobus x ayacahuite seed were harvested from about 5 minutes' pollination work. (Expected numbers of nonhybrid seeds due to wind-pollination were 8 and 4 respectively.)

For the other species the low seed sets are not typical of all trees in the area but are a consequence of the isolation of the particular trees worked. They are more abundant pollinators and usually give much higher seed sets when growing in groups. In these it is more difficult to find trees that do not need to be bagged.

Controlled Pollinations
--White Pines

Three criteria may be used to judge the success of the controlled pollinations--cone set, total seeds per cone, and filled seeds per cone. Little faith can be placed in the first two criteria, for two reasons. First, there is in many cases an inverse relationship between cone set or total seed set and filled seed set. Second, Buchholz (4) reports that in ponderosa pine the seed coat is fully formed before fertilization; if this is also true in the white pines the presence of the seed coat means merely that the pollen or pollen tube has provided a stimulating influence for cone and seed-coat production.

Judged by all three criteria, crosses between 5-needled pines of the section Cembra and hard pines or other pines of the subgenus Haploxylon were unsuccessful (tables 12, 13). Judged by the last criterion alone, crosses between species in different series of the section Cembra were unsuccessful or slightly successful, and most crosses within the series Strobi of the section Cembra were successful. Some interspecific crosses in the Strobi gave higher sets of filled seeds than did intraspecific pollinations on the same trees.

TABLE 12.--Relative success of different kinds of pollination in the white pines

Kind of cross	Tree x tree combinations		Average set of good seed per cone	Remarks
	Tried	Successful		
	Number	*Number*	*Number*	
Between sections*	5	0	0	No cones, or empty seeds.
Between species in different series	65	10	0-0.3	Normal cones, many empty seeds.
Between species in the same series	60	28	0-4.8	Normal cones, empty and full seeds.
Within species	50	27	1.0-10.0	Normal cones, empty and full seeds.

*Species, series, section, and subgenus limits as defined by Rehder (27).

TABLE 13.--Summary of results of controlled pollinations of white pine, 1947-50

(Pinus subgenus Haploxylon)

Female parent	Wind	Unpollinated control	Male parent: Self	Cembrae: koraiensis	Cembrae: cembra	Flexilis: Flexiles	Strobi: parviflora	Strobi: peuce	Strobi: griffithii	Strobi: ayacahuite	Strobi: strobus	bungeana: Gerardianae	Hard pines
flexilis	250 5 25 1.2 --	43 0 -- -- --				54 6 27 7.0 7.0			120 8 14 0 0		130 2 0.3 0 0		
parviflora	700 35 2.6 0.1 --		8 25 3.0 1.0 1.0		11 29 8.7 0 0	62 29 2.7 0 0	7 100 6.6 1.0 1.0	8 37 2.0 0 0	86 2 2.5 0 0		184 29 6.8 0 0		
peuce	19 90 11 0.8 --								15 67 18 0.5 1.2		19 79 26 3.7 5.4		
griffithii	500 20 12 3.9 --	25 12 0 0 --	5 60 20 12 12	16 19 10 0 0	28 18 1.0 0 0	21 5 0 0 0	19 16 18 0 0		53 13 17 10 46		289 12 26 2.1 9.2		
strobus	1200 30 2.1 0.7 --	157 27 0 0 --	84 14 16 5.4 6.4	658 31 4.5 0.3 1.0	344 33 6.0 .04 1.0	437 32 7.1 0.2 1.3	166 37 7.7 1.7 4.9	26 64 0.4 0 0	1013 32 5.0 1.6 4.3	267 27 7.4 4.8 13	572 34 3.1 2.1 24	66 21 0.1 0 0	54 28 0 0 0

Legend:

500	Strobili pollinated.
20	Cone set, in percent.
12	Number of empty seeds per cone.
3.9	Number of full seeds per cone.
6.3	Greatest set obtained of good seeds per cone.

Shading in corners indicates hybridization successful.

Crosses involving P. parviflora are an apparent exception. P. parviflora x griffithii consistently yielded few or no cones; P. strobus x parviflora yielded filled but non-germinable seeds.

The low seed yields on P. strobus to all types of controlled pollination is puzzling. The species was native within a few miles of Philadelphia, and now grows well in the area. Poor technique is probably not the reason, because open-pollinated seed yields for trees in groups are also very low. Possibly climatic factors are responsible. If so we may guess that climate limited the natural range of the species more by limiting seed yields than by influencing vegetative behavior or seedling establishment. At present there is no clue as to the nature of these climatic factors since the only really satisfactory seed yield (24.5 good seeds per cone) was obtained from branches that were left bagged from flowering until cone maturity--under just the opposite of natural conditions. The yields of filled seeds per cone were relatively higher in P. flexilis, P. griffithii, and P. ayacahuite, all of which are far removed from their native habitats.

Another peculiarity of P. strobus is that the total yield of seed per cone was usually less after intraspecific pollination than after pollination by some other species.

The performance of one large P. griffithii is interesting. It has yielded a maximum of 0.3 filled seeds per cone in each of 2 years of controlled-pollination work and has yielded little filled seed to open pollination (probably mostly self) the past several years. The few progeny obtained are weak and variable. The tree is old, vigorous, and apparently not a hybrid. A cytological irregularity is suspected but has not been checked.

Table 14 illustrates the variability encountered in making the same cross on different trees and in different years. A tree may be high-yielding for one cross and low-yielding for another one. This same variability was encountered in other crosses, particularly in the interseries cross P. strobus x flexilis, in which only 1 of 17 different tree x tree combinations was successful.

Our data were combined with those of other investigators to obtain table 15 and figure 1. The strength of the bond between any two species in figure 1 is presumably an indication of the closeness of their genetic and phylogenetic relationships. With the exception of P. lambertiana, all members of the series Strobi so far tested form a

closely knit group within which most crosses are possible. Maintenance of this series (with the probable exclusion of P. lambertiana) seems justified.

TABLE 14.--Variability in cone and seed set of fruitful Pinus strobus

Female parent *P. strobus*	Male parent						Wind		
	P. strobus			*P. griffithii*					
	1947-48	1948-49	1949-50	1947-48	1948-49	1949-50	1947-48	1948-49	1949-50
M7383	98 4.2	86 0.1	5 0	-- --	60 0	-- --	90* 0.6	90* 0.1	54* 3.6
M980	30 0	-- --	8 3.5	-- --	-- --	43 3.5	0 --	-- --	50 1.6
M7382	37 1.5	25 0	57 4.9	35 0.2	35 0.2	76 2.6	5 0	5 0	50 1.0
M831	65 0.8	-- --	18 0.2	67 0.8	-- --	3 0	60 0.1	-- --	10 1.8
G1638	-- --	93 0.4	8 1.0	-- --	74 0.1	26 4.3	-- --	90 0.2	31 2.5
All trees	57 1.5	37 0.5	18 3.8	30 0.1	30 0.1	33 3.1	50 0.3	50 0.1	23 1.0

*Cone sets to wind pollination are approximate.

Legend:

57 1.5

Cone set, in percent.
Number of filled seeds per cone.

Mayr (21) produces considerable evidence to show that in the animal kingdom geographic isolation is necessary for the maintenance of two closely related species. The species that cross readily are all geographically separated. P. lambertiana, whose range overlaps that of P. ayacahuite, is not closely related to the other species; it crosses little or not at all with them.

In respect to growth, the best white pines for the Philadelphia area are P. strobus, P. griffithii, P. ayacahuite, P. flexilis, P. koraiensis, and P. armandi, in decreasing order of probable value. The first three cross readily. Therefore concentration on selection and hybridization among these three species seems to be the most promising line of attack for the production of useful hybrids for the Northeast.

TABLE 15.--Summary of reported crosses in the genus Pinus, Section Cembra

Female parent	Male parent: Cembrae			Flexiles			Strobi										
	koraiensis	*cembra*	*albicaulis*	*flexilis*	*flexilis var. reflexa*	*armandi*	*lambertiana*	*ayacahuite*	*parviflora*	*peuce*	*griffithii*	*monticola*	*strobus*	*strobus var. chiapensis*	*peuce x strobus*	*griffithii x strobus*	*Species in other sections*
koraiensis			U 7				F 7						F 7				
albicaulis	F 4,7	F 4															
flexilis	F 7			H 6		U 4	U 4				H 4 F 6		F 4,6,7				
flexilis var. reflexa							F 7										
armandi				U 4 F 7	F 7		H 7						F 7				
lambertiana	H 4		F 4	F 7	F 7	H 4,7		F 4	F 4	F 4	F 4	F 4	F 4,7				F 4
ayacahuite											U 4						
parviflora				F 6,7					H 6	F 6,7	F 6	F 7	F 6 H 7				
peuce											U 6		H 6 U 7				
griffithii	F 6	F 6		U 4 F 6			F 4	H 2	F 6		H 6	U 4	U 4 H 2,6 7	U 7			
monticola	U 4					U 4	F 4	H 4	U 4 H 7	U 4	H 4		H 4,7		H 4		F 4
strobus	H 5 U 6 F 1,7	U 6	F 7	H 6 F 7		F 4,7	F 4,7	H 6	H 3,5,6 7	H 1,7 F 6	H 2,3,4 6,7	U 4 H 7	H 5,6				F 1,5,6
griffithii x strobus									U 7		U 4	U 4	H 7				
monticola x parviflora																U 7	
Species in other sections				U 4								F 4	F 4,5				

Legend: H -- Hybrids obtained
U -- Undetermined; possibly hybrids
F -- Failure

Authorities: 1. Johnson and Heimburger (19)
2. Rehder (27)
3. Sax (30)
4. Righter and Duffield (28)
5. Northeast. Forest Expt. Sta. (unpublished data, 1937-41)
6. Author's studies
7. A.G. Johnson (personal correspondence)

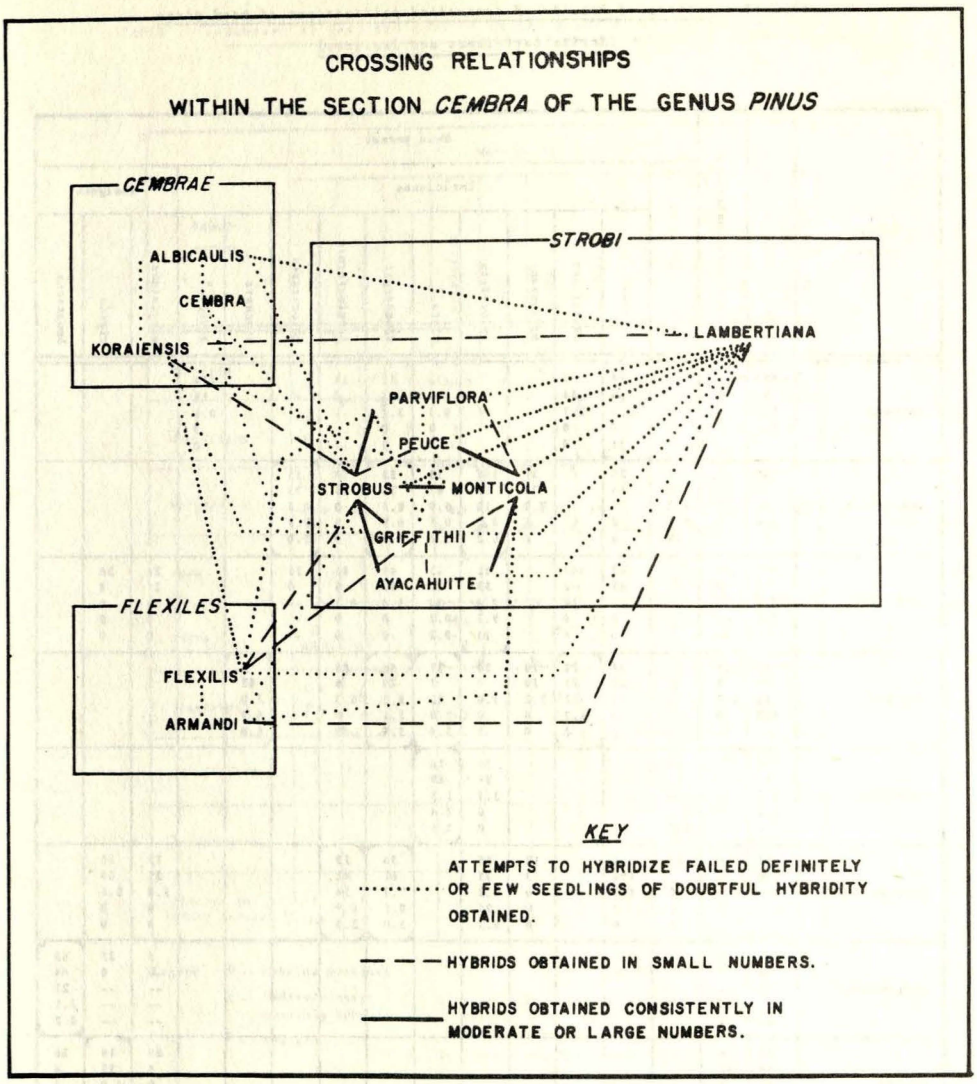

Figure 1.--The crossability pattern within the section Cembra of the genus Pinus.

Controlled Pollinations
--Series Lariciones

All four intraspecific crosses attempted were successful. However, seed sets to intraspecific crosses as well as to open pollination were rather low, possibly because of climatic control over seed setting.

TABLE 16.--Summary of results of controlled pollinations of hard pines (Series Lariciones and Insignes)

Female parent	Wind	Unpollinated control	Male parent: Self	Lariciones: *resinosa*	*densiflora*	*massoniana*	*sylvestris*	*nigra*	*thunbergii*	*tabulaeformis*	*taiwanensis*	*sinensis*	Mixture*	Insignes: *virginiana*	*rigida*	*banksiana*
resinosa	100 50 1.3 1.2 --			18 55 2.9 7.0 11	9 33 2.7 0 0			23 48 0.5 0 0	11 55 3.7 0 0	18 0 -- -- --			114 18 0.1 0 0			
densiflora	200 70 21 4.4 --	21 19 0 0 --	12 50 2.2 6.2 16	30 80 25 0 0		23 74 7.2 0 0	192 53 12 0.1 0.2	13 47 6.9 0.3 0.3	53 70 8.5 0.9 1.9	19 63 0 0 0	15 73 0.8 2.5 3.0					
sylvestris	700 40 2.1 2.2 --	53 0 -- -- --		48 25 13 0 0	104 52 12 0 0		61 33 2.5 9.3 11	43 23 24 0.2 0.2	40 20 5.4 0 0	86 6 0.3 0 0	15 0 -- -- --			28 25 0 0 0	26 8 0 0 0	
nigra	350 20 18 4.9 --	15 6 1.0 0 --		64 20 12 0 0	12 25 12 5.7 8.0	10 50 7.2 0 0	24 4 2.0 0 0	27 7 22 3.0 3.0	56 29 8.3 1.1 3.5	86 6 0.3 0 0		3 67 3.0 6.0 6.0				
thunbergii	12 50 1.5 0.8 --		20 45 2.8 2.3 2.3				21 81 3.5 0 0	16 69 1.3 2.4 2.5								
tabulaeformis	300 50 8.2 1.0 --	10 0 -- -- --	11 9 0 0 0	3 100 8.0 0 0		12 33 0 0 0	55 35 6.2 .05 0.3		36 61 7.2 0.5 2.0	19 42 14 1.9 2.0				13 31 5.8 0 0	11 64 0.6 0 0	
virginiana	40 50 18 6.7 --	14 0 -- -- --												5 0 -- -- --	25 0 -- -- --	63 44 23 0.1 0.2
rigida	20 50 43 9.0 --	6 33 0 0 --												25 4 0 0 0	19 58 4.0 62 92	26 4 0 0 0

*Mixture of pollens of all Lariciones available except *P. resinosa*.

Legend:

120	Strobili pollinated.
31	Cone set, in percent.
15	Number of empty seeds per cone.
3.2	Number of full seeds per cone.
5.4	Greatest set obtained of good seeds per cone.

Shading in corners indicates hybridization successful.

Of 30 different interspecific crosses tried, 8 were probably successful. In 6 of the crosses the seed sets were high enough to give some promise of being mass-produced in seed gardens. These results (table 16) are in substantial

TABLE 17.--Summary of reported crosses in the genus Pinus, Series Lariciones

Female parent	Male parent: *resinosa*	*densiflora*	*massoniana*	*sylvestris*	*mugo*	*nigra*	*thunbergii*	*tabulaeformis*	*taiwanensis*	*sinensis*	*Species in other series*
resinosa	H 6,7	U 6 F 7	F 7	F 2,6,7	F 6	U 4 F 2,7	F 6,7	F 7	F 7	F 7	F 2,6
densiflora	U 6 F 7	H 6	F 7	H 5,7	U 6	U 7	H 1 U 7 F 6	F 7	U 7		F 4,6
sylvestris	F 2,4,6 7	F 6,7		H 6,7	H 2	H 4 U 2,7	F 4,6,7	F 7	F 7		F 2,4,6 7
mugo	F 6	F 6					F 6				F 6
nigra	F 4,6,7	U 6,7	F 7	H 3 F 7		H 7	U 7 F 4	F 7		U 7	F 6
thunbergii	U 4 F 6	H 6		F 6,7		U 7					U 4 F 6
tabulaeformis	F 7		F 7	U 7			U 7	H 7			F 7
taiwanensis			U 4								
Species in other series	F 2,6	F 6		F 6		F 7	F 6				

Legend: H -- Hybrids obtained
U -- Undetermined; possibly hybrids
F -- Failure

Authorities

1. Hyun, S.K. (personal communication); Sargent (29). Natural hybrids common, female parent unknown.
2. Johnson and Heimburger (19)
3. Wettstein, W. von (personal communication); natural hybrid, female parent unknown.
4. Righter and Duffield (28)
5. Schreiner (33)
6. Northeast. Forest Expt. Sta. (unpublished data, 1937-41)
7. Author's studies

agreement with those of other investigators (table 17).

Crosses with species in other series were failures, as they were in most cases previously reported.

The crossability pattern is different from that found in the white pines. For one thing there appears to have been a greater amount of genetic (and taxonomic) differenti-

ation between species. For another, there is no closely knit group of species that cross readily with each other in all combinations. Too, some of the successful crosses involve species with slightly overlapping ranges (sylvestris-mugo, sylvestris-nigra, densiflora-thunbergii).

P. tabulaeformis is set apart from the rest of the series. As a female parent it yielded probable hybrids only with P. thunbergii. As a male parent it was ineffective in promoting cone or seed set on 4 other species.

P. resinosa is also set apart from the rest of the series. Even though it has been used intensively as a male and female parent by several investigators it has yielded probable hybrid seed from only two combinations. It is noteworthy that red pine is separated taxonomically from each of the other species in the series (except the Caribbaean P. tropicalis) in at least six characters (27, 36): American range; acuminate, ovoid bud; fascicles not spreading from branchlet; needles breaking when bent; resin ducts of needles both external and medial; conelet mutic; cone subsessile, leaving scales on the branch after dropping.

In the Philadelphia area P. resinosa, P. sylvestris, and P. nigra are the most promising as forest trees. P. densiflora and P. thunbergii also grow well but have very poor trunk and crown form. Since P. resinosa crosses little or not at all with the other species it appears necessary to treat it as a separate entity for improvement purposes. The other four species may be treated as a group within which gene exchange can be profitable.

Controlled Pollinations --Series Insignes

In each of 2 years the cross P. virginiana x banksiana resulted in high cone set, many empty seeds per cone, very few good seeds, and early germination of the good seeds. The cross, if possible at all, is not so easily made as are some of the crosses reported in the lodgepole-jackshore pine group by the Institute of Forest Genetics (28).

P. rigida is known to cross readily with P. echinata and P. taeda in the Australes and is probably a misfit in the Insignes (28). In view of this the failure of the interspecific crosses attempted is not surprising.

Criteria Of Hybridity

The following are the macroscopic differences observed in the first 1, 2, or 3 years in those lots believed to be true or probable hybrids.

P. densiflora x thunbergii, P. densiflora x taiwanensis, P. nigra x sinensis, P. thunbergii x nigra.--These are considered probable hybrids. In each case the seed set was consistent and greater than was to be expected from chance contamination. However, no growth differences between the hybrids and nonhybrid seedlings from the same female parent have yet shown up.

P. peuce x strobus.--Hybridity probable. Female parent not bagged but subject to little wind-pollination (mostly from P. strobus, slightly from self and two other species). Seed set increased nearly five-fold by additional hand-pollination. Seedlings from wind- and hand-pollination similar, vigorous, probably all of the same parentage. Seeds germinated nearly 100 percent.

P. peuce x griffithii.--Hybridity probable. Same female parent and pollinating conditions as in the previous combination. Seed set decreased slightly by hand-pollination. Seeds germinated 40 percent. One of the two seedlings obtained was red-stemmed soon after germination, unlike the seedlings in the previous combination; the other was dwarfed.

P. griffithii x strobus.--Hybridity probable. Seed set consistent from bag to bag. Seedlings have slightly redder stems in first weeks than do nonhybrids.

P. strobus x P. flexilis.--Hybridity certain. In the first year the hybrids were intermediate between seedlings of the parents in rate of germination, amount of damping-off, color of stem, and amount of leaf serration. By the third year they had the blue of the male parent. The seedlings lack vigor, possibly because of the particular tree used as a male parent. It is a poor specimen and its nonhybrid progeny are far below normal P. flexilis seedlings in vigor.

P. strobus x parviflora.--Hybridity certain. In each of two years only 4 out of 44 filled seeds germinated (germination is 95-100 percent in most P. strobus lots). The seedlings have much smaller cotyledons and leaves than do P. strobus seedlings, and lack vigor.

P. strobus x griffithii.--Hybridity certain. Cross repeated on different females with consistent results. Hybrids have redder stems in the first two weeks and slightly longer needles after a year than do nonhybrids. They are similar to nonhybrids in their second and third years.

P. strobus x ayacahuite.--Hybridity certain. Cross repeated on different females with consistent results. Some seed lots germinated significantly slower or less than did nonhybrid lots from the same female parent. Some seedling lots were greener in first weeks than nonhybrids. Similar to P. strobus seedlings at end of first year.

P. densiflora x sylvestris.--Hybridity certain. At end of first season hybrids have twisted secondary needles and are about 1½ inches tall whereas ordinary P. densiflora seedlings have only primary needles and are about 3 inches tall.

P. nigra x thunbergii, P. tabulaeformis x thunbergii, P. nigra x densiflora.--Hybridity probable. Seedlings taller than ordinary seedlings at end of first year.

SUMMARY

The techniques used in the forest genetics project of the Northeastern Forest Experiment Station from 1947 to 1950 are similar to those used by other workers, but many modifications making for greater ease of working were found possible without getting undue contamination from outside sources. Technique generally was not a limiting factor in obtaining high seed sets. Climatic factors and lack of species crossability were more important in most cases.

A large number of interspecific combinations were tried. The data from Acer, Pinus, and Fraxinus, when combined with those from other workers, are sufficient to warrant preliminary estimates of the crossability patterns in the genus.

In very few instances are the data sufficient to enable us to say that a certain cross will not take if repeated many times in many places. However, they show that in these genera many crosses between closely related species will give from 10 to 100 percent of the seed expected from intraspecific pollinations, whereas crosses between less closely related species give no seed or at the most up to

5 percent of the possible seed set. The successful and probably successful crosses are listed below:

ACER

Crosses within species all easily made.

A. platanoides x mayrii.--Hybridity certain. Grows same rate as female parent. Seed set moderate.

A. platanoides x cappodocicum.--Hybridity certain. Hybrids vigorous, seed set moderate.

A. platanoides x saccharum and reciprocal.--Hybridity probable. Seed set low.

A. saccharum x nigrum.--Hybridity certain. Possibly a backcross. Seedlings similar to female parent, seed set high.

A. rubrum x saccharinum.--Hybridity certain. Seed set high.

A. negundo x henryi.--Hybridity certain. Grows faster than female parent, possesses foliage characters of value as an ornamental.

FRAXINUS

Crosses within species easily made on fruitful trees but many failed because of accidents.

F. pennsylvanica x velutina and reciprocal.--Hybridity certain. No growth differences as yet. Seed set very high.

LIRIODENDRON

Liriodendron tulipifera.--Crosses within species easily made but filling of seed was low and variable, although surpassing filling of open-pollinated seed. No interspecific crosses tried.

QUERCUS

Crosses within and between species all made with difficulty, with very low seed sets.

Quercus borealis x velutina and reciprocal.--Hybridity certain. Hybrids do not surpass parents in growth.

ABIES

Results of pollinations doubtful because of difficulties (now solved) of testing filling of seed and obtaining adequate germination.

PICEA

Crosses within species apparently easily made with moderate seed sets. Most interspecific crosses failed.

P. abies x asperata.--Hybridity certain. Young hybrids not easily identifiable. Seed set high.

P. montigena x abies, P. montigena x asperata.--Hybridity probable. Seed sets high.

PINUS

Crosses within species made with varying degrees of difficulty, depending mainly on fruitfulness of female parents.

P. peuce x strobus.--Hybridity probable. Seed sets high.

P. peuce x griffithii.--Hybridity probable. Hybrids runty, seed set low.

P. griffithii x strobus and reciprocal.--Hybridity certain. Hybrids probably superior to parents in growth. Seed set moderate to high.

P. strobus x flexilis.--Hybridity certain. Hybrids intermediate in four characters. Cross took in only 1 of 17 combinations tried. Seed set low.

P. strobus x ayacahuite.--Hybridity certain. Seed set moderate to high.

P. strobus x parviflora.--Hybridity certain. Seedlings weak. Seed set high in one combination.

P. densiflora x sylvestris.--Hybridity certain. Seed set low. Hybrids indentifiable the first year.

P. densiflora x taiwanensis.--Hybridity probable. Seed set moderate.

P. densiflora x thunbergii.--Hybridity probable. Seed set low.

P. nigra x densiflora.--Hybridity probable. Seed set moderate.

P. nigra x thunbergii.--Hybridity probable. Seed set moderate.

P. nigra x sinensis.--Hybridity probable. Seed set moderate.

P. tabulaeformis x thunbergii.--Hybridity probable. Seed set moderate.

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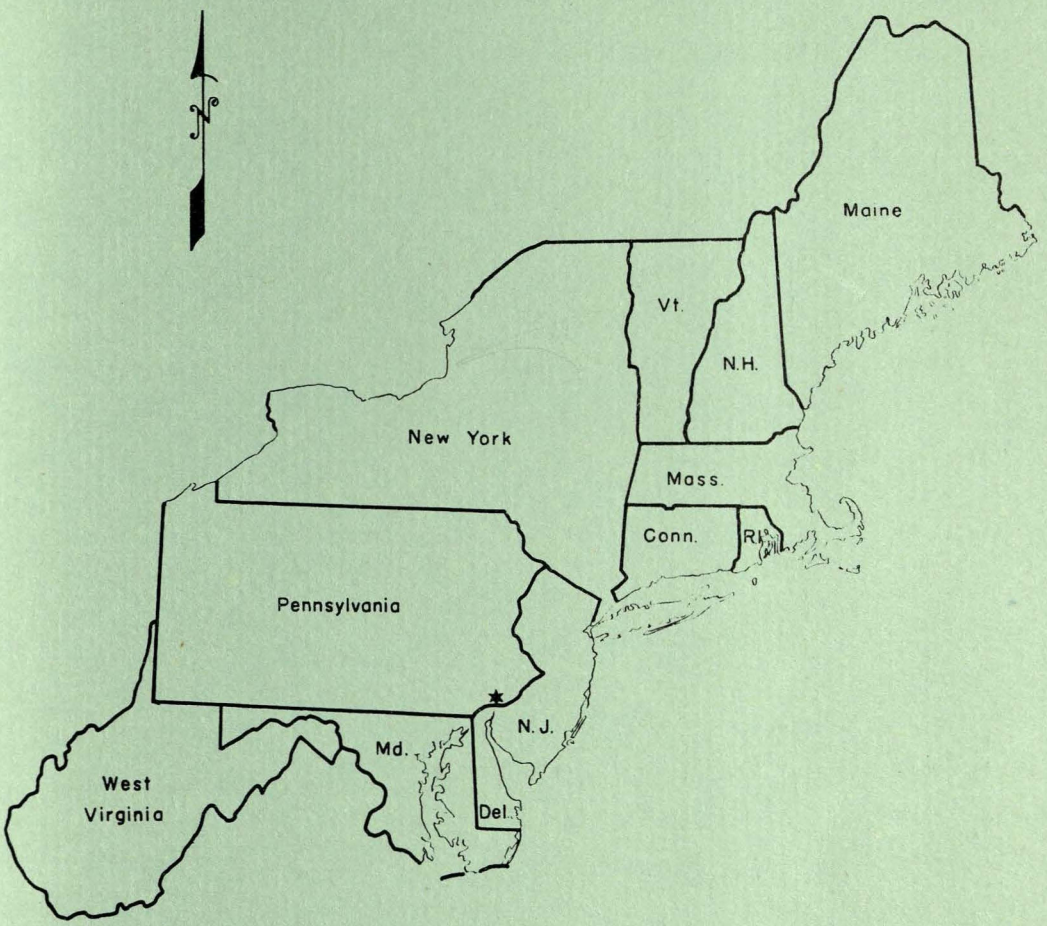

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